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V. Conspicuous Effects on the markings and colouring of Lepidoptera caused by exposure of the pupæ to different temperature conditions. By FREDERIC MERRIFIELD, F.E.S.

[Read December 3rd, 1890.]

PLATE IX.

In reviewing the results of my temperature experiments of last year, I found some which could not altogether be explained by the simple theory that a moderately low temperature, applied to the pupa for a certain minimum period, caused in the imago darkness of colouring or a change of markings in a definite direction. In particular they indicated that the part of the pupal period during which the temperature was applied might have much to do with the result, and therefore I determined to conduct experiments specially directed to ascertain whether there was such a period, and, if so, to define it. During the earlier part of this investigation I was under the impression, derived from the accounts of experiments by other observers, that the earliest stage of the pupal period was the sensitive time, and, at all events, that the last few days were of little importance; and accordingly, in certain elaborate experiments which I made, consisting of the forcing of pupæ immediately after pupation for periods differing by a few days, followed by cooling for different periods; and the converse, -i.e. cooling succeeded by forcing, -I generally finished in both cases by forcing the pupa for a few of its last days, as a matter of convenience, in order to get it out of the way for further work. Some facts observed, however, during the early part of the past summer, led me to suspect that for certain effects the later days of the pupal period were especially important, and I instituted accordingly some experiments directed to ascertain whether it was so.

I tried these with the two species I had before found sensitive to temperature,—namely, S. illustraria (tetralunaria) and E. autumnaria,—and the results fully con-

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firmed my suspicion. I obtained more striking results than before, and the fact was brought out that the change of markings due to temperature was caused by temperature conditions so different from those which caused colouring, or darkness, that it became possible artificially to produce either effect with little or no admixture of the other; so, for example, as to get from the same brood of an insect which is subject to seasonal dimorphism what may be termed, speaking generally, four distinct temperature varieties, viz., (1) summer markings with summer colouring, (2) summer markings with an approach towards spring colouring, (3) spring markings with summer colouring, (4) spring markings with spring colouring. It will be seen that all these results have been more or less fully obtained; three of them from a single brood, and the fourth from another precisely similar brood, might certainly have been obtained from the first brood had a portion of it been subjected to the appropriate treatment.

When I use the term spring and summer markings or colouring (in which last word I include lightness or darkness of hue) I am only speaking generally. I have not yet, I think, met with a case where the summer moth has been made to assume the exact colouring of the spring insect, but, as regards markings, I think the resemblance is complete, or nearly so.

For purposes of description, it has been found necessary to divide the pupal period into four stages, the duration of each of which greatly depends on the temperature, viz.; —(1) the soft condition, which, at ordinary summer temperature, continues about twenty-four hours or less; (2) the central inactive condition, which may last for a few days only or for many months; (3) what I would term the penultimate stage, being that separating the inactive period from (4) the last stage, commencing when the colours of the pupal insect begin to show. Each of the stages (3) and (4), at the summer temperature, seems to last, in the two species experimented on, two or three days, but at a lower temperature can extend over several weeks.

The icing temperature may be taken as a steady 33° Fahr. (subject to the qualification that from about the beginning of July of this year to the 10th August, during which the pupe, instead of being in an ice-box, were placed under the bottom of the ice-holder in the refrigerator, it ranged from about 35° to 39°); the "cooling" temperature, being that of the interior of the refrigerator, ranged from 39° to 55°, averaging in summer about 47°: the forcing temperature was about 80°. The "out-door" and "room" or "in-door" temperature, especially the former, varied, but I give the amount of it, as far as practicable, in each case.

I may premise that (with the aid of an assistant) I have tried many more experiments than I describe here; some necessarily gave negative or inconclusive results, and with these, though useful to myself, I will not trouble the Society.

It will perhaps be remembered that last year's experiments showed that a naturally rather dark-coloured brood of illustraria of the summer emergence, when subjected to icing for periods successively lengthened by fourteen days, produced moths darker in colour, and, after a period averaging twelve weeks or more, for the most part distinctly altered in markings so as to approach those of the spring emergence. This year I determined to experiment with broods from a race selected for its tendency to light orange or chestnut colouring, which, to give it a short distinctive name, I called "red," and which, being of a lighter colour, would be better adapted to show dark effects.

EXPERIMENTS ON ILLUSTRARIA.

For this purpose I took two broods of the spring larvæ of the 'red" race, forcing the larvæ to get them out of the way of other experiments, and they pupated between 10th and 25th June. The first of these I called "red c"; it produced me about 59 pupæ.

Ten of these "red c," taken promiscuously from day to day, were forced at the temperature of 80°, and produced eight moths, all of the light warm tint proper to the race, and in all respects of marking and colouring belonging to the summer type. Two of them are shown as Figs. 3 and 4 in the Plate.

The rest were iced from day to day as they hardened, and on the 14th Sept., i.e. after about twelve weeks' icing, were taken out of the ice-box and subjected to differential treatment as follows :---

(1) Icing twelve weeks followed by forcing.—Twenty-three were thus forced, and after five days' forcing they began to emerge. Nine came out on the fifth day; the rest were then beginning to show the colour of the perfect insect, and would doubtless have

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emerged on that day or in the next day or two. Ten of them were placed at the "cooling" temperature, then averaging 43° , and five of these, besides some cripples, emerged in from two to eight days. Of the remaining thirteen, eleven emerged uncrippled or nearly so. There is no material difference between those which were thus differently treated. They show an interesting combination of colouring and markings, viz. a colouring approximating to that of the summer emergence with, in all but 2 or 3 individuals, the markings proper to the spring emergence. Nos. 5 and 6 in the Plate are typical examples of them.

This experiment seems to show (1) that though icing the summer pupe for twelve weeks develops in general the spring markings, yet that after the change in markings has thus been effected, forcing during the last five days brings out the moths in the characteristic summer colouring; (2) that exposure to a low temperature (about 43°) when the insect is in the ultimate pupal stage, *i.e.* when the colours of the imago are beginning to show, makes no difference.

(b) Icing twelve weeks, followed by a low or moderate temperature.—The remainder of the "red c," twenty-six in number, were on the 14th Sept. placed out of doors, and all emerged in from nine to sixteen days, the temperature at 8 a.m. averaging about 57°. They showed not only the spring markings, but, as will be seen in the Plate, figs. 7 and 8, a dark colour, in some cases closely approximating to that of the spring emergence. With two or three exceptions, all are darker than any of those in the preceding experiment, and most are much darker. We thus have the spring markings and a close approximation to the spring colouring produced by subjecting to a moderately low temperature, averaging 57° at 8 a.m., pupse the moths from which would otherwise have shown the markings and colouring proper to the summer emergence.

Three of the twenty-six were, after eight days of the out-door temperature "cooled" (43°) emerging respectively in 12, 16 and 30 days; but this treatment made no appreciable difference in their appearance.

(c) The same, succeeded by forcing during the ultimate period. —Four of the twenty-six were after eight days forced, and three of them emerged in from $1\frac{1}{2}$ to $2\frac{1}{2}$ days; in two of these there is a change in a direction towards the summer colouring.

Taken as a whole, the experiments on "red c" seem to show that the ordinary out-door temperature of a rather warm September, which, taken at 8 a.m. during the time of exposure, averaged about 57°, is as efficacious to produce a dark colouring as

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is the much lower "cooling" temperature (of 43°), but that exposing the pupa *during its last two or three days* to a forcing temperature may be enough to affect the colouring in the opposite direction.

Period of pupal development when temperature operates on colour.—The next experiments were made with the object of endeavouring to define still more closely the period of pupal development during which the temperature has to be applied in order to develop its effects on colouring. For this purpose the second "red" brood, distinguished as "red a," which had been at the icing temperature for about fourteen weeks, was taken. Eight moths, the pupæ of which had been forced from the time they hardened, are scarcely to be distinguished from the "red c" similarly treated, being of the same light warm tint, and with the usual summer markings. Of those not so forced I had about seventy pupæ. This brood, however, was not so healthy and vigorous as the "red c's". Whether from this or some other cause, the differences in colouring caused by the treatment are not so marked as in "red c."

It should be premised that all the experiments on *illustraria* under heads (d) and (e) subsequently detailed were tried with summer pupze which had been iced about fourteen weeks, a treatment which, as already shown, appears to affect the markings rather than the colouring.

Fourteen male and fourteen female pupz were, on the 25th Sept., taken from the ice and divided into two parts, and were then treated as follows :---

(d) Forcing for different periods succeeded by a moderately low temperature.-With the first division, consisting of six males and six females, the experiment was tried of first forcing and then from day to day removing into the open air, which at 8 a.m. averaged about 56°. From the Table (I.) appended it will be seen that they were, when taken from the ice on the 25th, ready to emerge in about five days of a forcing temperature. This indicates that the pupal period, measured by the progress made, was then not quite half over, for I have found that the summer pupa exposed to a forcing temperature usually emerges in from eight to ten days. The results were as follows :- Nos. 1 3 and 2 3, and Nos. 1 2 and 2 2, which had been deprived of a forcing temperature during two or three out of their last five days, are decidedly darker than the others; of the remainder, No. 3 3. which had been deprived of but one day's forcing, is lighter, No. 5 3 was accidentally lost, and No. 6 3, which was forced the whole of the five days, is almost of the summer colouring of the

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parents which had been forced all through. There is little difference between the females Nos. 3, 4, 5 and 6, two of which are slightly crippled; in general they are nearer to the spring than the summer type of colouring.

(e) Moderately low temperature for different periods followed by forcing.—With the second division, consisting of eight males and eight females, the converse experiment was tried by placing the pupze, when taken from the ice, in the open air, and removing them at intervals to the forcing-box. The intervals were of two or three days, instead of a single day, in order to make allowance for the slower rate of progress at a lower temperature. The results are recorded in Table II. They fully confirm the results of the experiment last recorded. Of the males, Nos. 1, 2, 3, 4, and 5, all of which had had from one and a half to four days' forcing, approach the summer colouring, and there is not much difference between them; No. 6, with only one day's forcing, is darker. Nos. 7 and 8, with no forcing at all, are decidedly darker. Of the females, Nos. 7 and 8, with no forcing at all, are decidedly darker than Nos. 1, 2, 3, 4, and 5, which had had from one to three and a half days' forcing.

The last class of experiments was repeated with pupe from another brood not of the "red" type, offspring of a brood kindly reared for me by Mr. Hollis, but of a more ordinary and variable colour. They were contemporaries of the "red a," and fourteen of them were treated in exactly the same way, six males and six females being in the same manner selected for first forcing and then outdoor exposure, and eight males and eight females for outdoor exposure first and then forcing. The results are in the same direction, though not so marked. The experiments with "red a" and with the last-named brood showed that about three days of a temperature averaging 56° were equivalent, in the rate of pupal progress, to one day at 80°.

The general result of the experiments on the three last-mentioned broods may be stated to be that from two to three days' forcing during the last parts of the pupal stage may be enough to affect the colouring, and in many cases to a very marked degree.

(f) Ordinary indoor temperature, followed by low temperature. —Another experiment, partly founded on an accidental occurrence, shows corresponding results, from the exposure of part of a summer brood to the lower "cooling" temperature. A red brood of the third generation, fed up rapidly, and rather unexpectedly pupated before the middle of August. They were brought indoors, where more than a dozen were found to have emerged on the 21st August at the ordinary temperature of the room. The remainder were

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then placed in the refrigerator, where by the 6th September twenty more had emerged. All are slightly darker than their forced red parents of the second generation, but such as emerged after the 15th September, *i.e.*, after twenty-six days of the low temperature, are decidedly darker than the others. A light uncooled male and another cooled are given as Figs. 1 and 2 in the Plate.

The conclusions to be drawn from this experiment seem to be (1) that keeping the pupe at the ordinary room temperature, probably about 65° to 70°, made the moths slightly darker than their parents, which were forced; (2) that at the low temperature of the refrigerator, averaging at this time, I should think, about 43°, three or four weeks did not represent, in pupal progress of development, more than two or three days of a forcing temperature, the lower temperature, as in the other cases, producing a darkness of colouring.

In connection with the effect produced by moderate differences of temperature, I may here mention that in two broods of *illustraria* pupe, kindly brought up for me by Mr. Weldon at Plymouth, and kept indoors, some that emerged within a day or two of their arrival in June and July are conspicuously darker in colouring than the rest of the broods which were forced. I should think it improbable that the unforced ones had been at a lower average temperature than 60° .

EXPERIMENTS ON E. AUTUMNARIA.

The other systematic experiments tried were with E. autumnaria. Dr. Chapman kindly sent me two large batches of eggs, the moths from which I found, after a few had been forced, were very similar; and after a time I mixed the larvæ.

(g) Forcing all through, or brief cooling followed by forcing.— Some were forced all through as pupe; others were cooled for 3, 7, 10, 14, 17, and 21 days, then forced, emerging in from 10 to 15 days of the forcing temperature. Thirty moths emerged (rejecting cripples). There are considerable individual differences among these, but the only great difference of a general character is that after about 14 or 17 days' cooling the colouring and markings are less vivid, the ground colour is dulled, the spotting blurred, the outer line broadened, and the inner line shows a tendency to disappear.

(h) Cooling, followed by an ordinary indoor temperature.— Others, after being cooled for 7, 10, 14, 17, 21, and 28 days were then, instead of being forced, kept at the ordinary temperature of the room, averaging, I think, about 65° to 70° in July, till they emerged, which they did, to the number of 20 (rejecting cripples), in from 18 to 21 days. These, also showing considerable individual TRUNG ENT SACE LOWE 1891 — PAPET L (MAPPEN).

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variation, are, as a rule, very decidedly darker than those which had been finally forced, viz. (g).

(i) Cooling five or six weeks, followed by forcing.—Other larvæ were sleeved, and pupated during the first three weeks of August. They were "cooled" within a few days after pupation, and taken out of the refrigerator on the 14th September, *i.e.*, after about five or six weeks, and forced, emerging in from six to eight days (a few of them being taken out of the forcing-box, and replaced in the refrigerator when the colouring of the perfect moth began to show; there is no marked difference in those so treated). The colouring of all, though dull, is not particularly dark, decidedly not so dark as in those of experiment (h). About twenty emerged (rejecting cripples).

(j) Cooling five or six weeks, followed by different temperatures.—Others, which had been cooled for five or six weeks, were afterwards placed at the ordinary outdoor temperature, averaging about 56° at 8 a.m., emerging in from $12\frac{1}{2}$ to 21 days, some of them being on the eighth day placed at the "cooling" temperature, and emerging in from $2\frac{1}{2}$ to $16\frac{1}{2}$ days more; others, being on the eighth day forced, and emerging in from $2\frac{1}{2}$ to 5 days afterwards. About sixteen emerged (rejecting cripples). Nearly all, except those thus forced, are dark, most very dark; those cooled being little, if at all, darker than those left at the ordinary temperature.

The tendency to dulness, to the blurring of spots and broadening of the outer line, and to the disappearance of the "inner line," is to be remarked in most of these included in experiment (j).

Figs. 11 and 12 in the illustration represent those that were forced without any or very brief previous cooling (g); Figs. 13 and 14, those cooled several weeks, and then forced (i); Figs. 15 and 16, those cooled several weeks, and then placed at a low, or moderately low, temperature till emergence (j).

EFFECTS OF MOISTURE.

Some experiments in 1888 seemed to show no difference in markings or colouring between pupe of *illustraria* kept moist, and others in a quite dry atmosphere. This year I placed two lots, each of six pupe of *autumnaria*, as soon as they had hardened, on sand kept wet in jam-pots covered with closely-fitting pieces of glass, one jam-pot (experiment k) being placed in the refrigerator 28 days, and then in the room, till the moths emerged, which four of them did in from 17 to 19 days more (two having died); the other (experiment l) in the forcing-box, where five out of the six emerged in from 12 to 16 days. Afterwards (experiment m) four

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more pupe were placed in a flower-pot on wet moss kept saturated with water, and covered with a piece of glass and placed out of doors; all emerged, two being cripples. Similar experiments (experiments n and o) to the first two were tried with two divisions, respectively of five and six summer pupze of illustraria, all of which emerged, two being somewhat crippled. Two autumnaria, out of those kept moist, are slightly darker than the average of those kept dry, though not so dark as some of these. With that exception, if it be one, there is no appreciable difference in the case of that species, and none in *illustraria*, between such as were kept moist and such as were kept dry, but were in all other respects similarly treated. These results do not support the theory that exposure of the pupe to moisture darkens the colour of the imago. I do not of course doubt the observations made which tend to show that some insects bred in moist situations are generally darker than the same species bred in drier localities, nor do I fail to recognise the great weight attaching to the opinion on this subject of some highly qualified authorities; indeed, it appears to me probable that, especially in countries where the difference of seasons is rather that between wetness and dryness than between warmth and coldness, moisture affects colour; but I would venture to make the remark that I believe most of the English Lepidoptera on which this effect has been observed emerge in the summer, and that wetness in summer, whether owing to a rainy mountainous locality or to the occurrence of a rainy season, causes a relatively low temperature; and it has been shown that the difference of temperature between a warm English summer and a cool one is sufficient to produce a very substantial darkening effect.

EXPERIMENTS WITH OTHER LEPIDOPTERA.

(p) At the end of June a few recent pupe and pupating larve of V. *urticæ*, all probably from the same brood, were given to me by Mr. Vine; some were placed at 80°, and others in the refrigerator at about 47°. Three of the former emerged in seven days; one of the latter after five weeks' cooling. It differs materially from the other three, the darker patches and the blue crescents having spread considerably, and the ground colour being duller.*

^{*} This is open to the observation that it is the case of a single individual, but the inference from it is much strengthened by the statement of Mr. Jenner Weir, in the discussion which followed this paper, that so dark an example of this common European species is rarely met with, and by the statement (see Weismann's 'Studies in Heredity,' by Meldola) that the species becomes black in northern latitudes.

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(q) B. quercus.—Experiments with this species have not yet been brought to a conclusion, but I have had out a number of the var. callunæ, from Aberdeen and Perth, at a forcing temperature; and these are certainly lighter in colouring than the ordinary callunæ, and not greatly to be distinguished from the ordinary B. quercus.

GENERAL CONCLUSIONS.

All the experiments, so far, seem to point to the conclusions :---

1. That both the markings and the colouring of the perfect insect may be materially affected by the temperature to which the pupa is exposed.

2. That the *markings* are chiefly affected by longcontinued exposure, probably previous to the time when the insect has begun to go through the changes between the central inactive stage and emergence.

3. That the *colouring* is chiefly affected during the penultimate pupal stage, *i. e.*, before the colouring of the imago begins to show.

4. That a low temperature during this penultimate stage causes darkness, a high temperature during the same period having the opposite effect.

5. That, in the species operated on, a difference between 80° and 57° is sufficient to produce the extreme variation in darkness caused by temperature, a further lowering of the temperature having no further effect on it. (Taken in connexion with the others, previously published, these experiments show further that nearly the full effect in colouring may be produced by a much narrower range of temperature, viz., from 76° or 80° to 65° in autumnaria, from 73° to 60° in illustraria.)

6. That in these species dryness or moisture during the pupal period, whether during a low temperature or a high one, has little or no effect on the colouring of the imago.

These conclusions may be treated as established as regards *illustraria* and *autumnaria*. Of course a much larger number of species should be tried before they can be treated as applicable generally. I do not doubt that protective requirements, hereditary tendencies, and probably other climatic conditions than those of temperature, and other causes that need not be enumerated, have their part in affecting colour; but the facts ascertained certainly point to the probability of some general connection between the temperature during the pupal period and the colouring of Lepidoptera. As regards the species experimented on by me, however, though I am satisfied that temperature is the chief cause of the general changes of colour, as distinguished from individual variations produced, there are certain slighter variations of a general character which rather indicate that other external influences also operate; and these, I hope, may be made the subject of further investigation.

The results obtained appear also to indicate that probably some local climatic varieties, and even seasonal varieties, may be found to be, in part at least, temperature forms of the individual; and, looked at from this point of view, they appear to me to lend some support to Lord Walsingham's theory as to the advantages derived by an insect in a cold region from being of a dark colour, for they show that, if that is an advantage, it is one that can be acquired, not only by a race for use in a cold locality, but by individuals for use in a cold season. I think it quite clear that if a cool week supervened in Southern England between the beginning and the middle of July, or a hot week in the middle of April, at either of which times many of the pupe of illustraria would be in what I have called the penultimate pupal stage, most of these insects which it found in that stage would have their colouring affected. It would appear that even two or three hot days, if they came exactly at the right period, would be enough for the purpose; and I need hardly observe that it is very unlikely that these are the only species that would be so affected.

There is another general suggestion which I venture to make in concluding. If Prof. Weismann's theory is accepted, that the existing forms of most European and some North American Lepidoptera have come to us from a glacial period or climate, and that icing the pupa causes the insect to "throw back" to its earlier form, then experiments, of the kind tried, on the pupe might assist us in tracing the evolution of the markings on the wings of some of the most highly developed modern forms.

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P.S.-Note.-March, 1891. I am now able to add that the colouring of the spring emergence of illustraria is as much, or nearly as much, affected by temperature during the penultimate pupal period as is that of the summer emergence. This has been established in the case of three different broods, portions of each having been subjected to temperatures of 60° and 80° respectively; the latter often in colouring very closely approach the light chestnut-orange summer type. This is interesting in reference to Prof. Weismann's theory, that in cases of this kind the moth from the summer pupa can be caused to resemble that from the winter pupa, but not vice versa, as it shows that either form is equally ready, on the suitable temperature stimulus being applied, to assume the characteristic appearance of the other, so far as colouring is concerned. In other respects my observations are in accord with that theory. Thus, I have never been able to cause the moth from the winter pupa to take the *markings* proper to the moth from the summer pupa, whereas the moth from the summer pupa can be made in markings to resemble almost exactly that from the winter pupa; nor have I been able to cause the moth from the winter pupa to emerge in a period approaching in brevity that of the summer pupa; indeed, in the great majority of cases, the early and continued exposure of the winter pupa to a temperature of 80°, or even 60°, caused its death.-F. M.

EXPLANATION OF PLATE IX.

S. illustraria.

FIG. 1. Summer brood, *f*, not cooled.

2. Same brood, 3, cooled in its later pupal stages.

- FIGS. 3 (3), 4 (2). Summer brood, forced at 80° till emergence. 5 (3), 6 (2). Same brood, iced 12 weeks, then forced at
 - 5 (3), 6 (9). Same brood, iced 12 weeks, then forced at 80° till emergence.
 - 7 (3), 8 (9). Same brood, iced 12 weeks, then placed at about 57° till emergence.
 - 9 (3), 10 (2). Examples of ordinary spring emergence.

The resemblance of Figs. 5 and 6 to Figs. 3 and 4 in colouring, to Figs. 7 and 8 in markings, will be noticed.

E. autumnaria.

- FIGS. 11 (3), 12 (\mathfrak{P}). Forced at 80° till emergence.
 - 13 (3), 14 (9). Iced 5 weeks, then forced at 80° till emergence.
 - 15 (3), 16 (2). Iced 5 weeks, then placed at about 57° till emergence.